

**HERBIVORY BY SPECIES OF *TRIRHABDA* (COLEOPTERA:
CHRYSOMELIDAE) ON *SOLIDAGO ALTISSIMA*
(ASTERACEAE): VARIATION BETWEEN YEARS**

OWEN D. V. SHOLES

Division of Natural Sciences and Mathematics, Assumption College,
Worcester, Massachusetts 01609.

Abstract.—Larval and adult *Trirhabda* beetles were more abundant on *Solidago altissima* than on *S. juncea*, and more abundant on both goldenrod species in 1977 than in 1976. Heavier herbivory by species of *Trirhabda* in 1977 stunted the growth and retarded the flowering of *S. altissima*, as compared to 1976; *S. juncea*, with almost no damage by *Trirhabda* species, bloomed earlier in 1977 than in 1976. Despite *Trirhabda* and other abundant herbivores, *S. altissima* is the dominant old-field goldenrod in the region of Ithaca, New York. Years with low densities of *Trirhabda* species may contribute to the success of *S. altissima*.

Several species of the genus *Trirhabda* LeConte feed on *Solidago* L. both as larvae and as adults (Balduf, 1929; Blake, 1931; Capek, 1971; Hogue, 1971; Reid and Harmsen, 1976; Sholes, 1977; Messina, unpublished data). *Trirhabda borealis* Blake was the dominant herbivore on *Solidago canadensis* L., based on biomass and numbers of individuals, at two sites in southern Ontario; however, Reid and Harmsen (1976) did not observe any "obvious, serious defoliation of *S. canadensis*" by species of *Trirhabda* in their study sites, and only rarely elsewhere. Serious defoliation was observed elsewhere in Ontario (Capek, 1971) by larvae and adults of *T. borealis*, and in Ohio (Balduf, 1929), where the larvae of *T. canadensis* Kirby sometimes consumed "much of the foliage" of *Solidago* plants. In this paper, I compare two years of observations of herbivory by *Trirhabda* species on *Solidago altissima* L., a close relative of *S. canadensis* (Fernald, 1950).

THE GENUS *TRIRHABDA*

Beetles in the genus *Trirhabda* (Chrysomelidae: Galerucinae) are often found on goldenrods; of the 22 or 23 species in North America (Blake, 1931; Hogue, 1971), at least eight feed on *Solidago*. The species found near Ith-

aca, *T. virgata* LeConte and *T. borealis* (Sholes, 1980; Messina, unpublished data), are 6–12 mm in length as adults, with an individual dry weight of about 9 mg. The larvae are shiny blue-black dorsally, tan ventrally, and grow to about 10 mm in length. Larvae are found on growing goldenrods in the spring, feeding there until they drop to the soil and pupate in middle or late June. Adults eclose in late June or early July and can be found on *Solidago* from then until late September. Mating occurs on the plants, and the females oviposit in the bases of broken *Solidago* stems; the eggs overwinter and hatch the next spring. Thus, the species are univoltine, and are active through nearly all of the growing season either as larvae or adults (Balduf, 1929; Blake, 1931; Messina, unpublished data; Reid and Harmsen, 1976).

FIELD SITES AND METHODS

As part of a study concerning the arthropod fauna of *Solidago juncea* Aiton and *S. altissima* (Sholes, 1980), I periodically censused *in situ* the arthropods occupying panicles (in 1976) and whole plants (in 1977) of these goldenrods in two old fields near Ithaca, New York.

Field 1, where I studied *S. altissima*, is centered at 76°24'52"W, 42°23'16"N. The elevation is about 258 m, and the slope less than 3% on either side of a 5–10%-slope ridge running the length of the field. Field 2, in which I studied *S. juncea*, is centered at 76°25'54"W, 42°29'36"N. The elevation is about 340 m, and the slope 3% or less (see Sholes, 1980).

In 1976 I established 10 random points in a 20 × 50 m quadrat, then marked the goldenrod plant nearest each point that showed flower bud development and repeated the same process in four contiguous areas for a total of 50 plants in a 50 × 100 m area in each field. I censused *S. juncea* 16 times between 17 July and 6 October, and *S. altissima* 11 times between 17 August and 13 October. In each census, I counted all the arthropods on the panicles of every marked plant while disturbing the plants as little as possible. In each field, 48 plants survived through all the censuses (two in each field were broken off at the ground by large animals).

In 1977 I established 20 points spaced randomly along a 50 m transect running between the midpoints of the 100 m sides of the 50 × 100 m area in each field, then marked the plant showing bud development nearest each point. I censused *S. juncea* 14 times between 10 July and 12 October, and *S. altissima* 9 times between 19 August and 21 October. In these censuses, I counted the arthropods on the entire above-ground plant, noting whether they were on the panicle, or on the stem below.

I measured the height of each plant, the distance to the nearest conspecific plant (decimeters between stem bases), and at each census, the percent of the heads in bloom, the volume of the panicle (the smallest rectangular space containing the entire inflorescence), and the distance to the nearest

Table 1. The number of *Trirhabda* adults on *Solidago* plants in 1976 and 1977 and the height and blooming date of these same plants.

	<i>Solidago</i> Species	1976 (n = 48)	1977 (n = 20)	P ¹
No. of <i>Trirhabda</i> per liter of panicle space	<i>S. altissima</i>	13/1,382 = .009	10/456 = .022	
	<i>S. juncea</i>	0/2,909 = 0	1/775 = .001	
No. of <i>Trirhabda</i> per plant	<i>S. altissima</i>	—	67/180 = .372	
	<i>S. juncea</i>	—	2/280 = .007	
Ht. of plants ($\bar{x} \pm s$) (cm)	<i>S. altissima</i>	118 \pm 23	79 \pm 19	<.001
	<i>S. juncea</i>	85 \pm 18	71 \pm 14	<.005
Peak date of blooming ($\bar{x} \pm s$)	<i>S. altissima</i> ²	16 Sept. \pm 6 days	20 Sept. \pm 4 days	<.01
	<i>S. juncea</i>	24 Aug. \pm 7 days	20 Aug. \pm 7 days	<.05

¹ P values for two-tailed Student's *t*-test; blanks indicate no test was done.

² Variances unequal ($P < .05$) using *F*-test; modified *t*-test for unequal variance used here.

blooming conspecific. Using percent blooming over time, a peak date of blooming was interpolated for each plant, and the mean, variance, and standard deviation were calculated for the peak blooming of each sample population (Sholes, 1980).

I observed the kinds of damage done by the feeding of *Trirhabda* larvae and adults on *Solidago*, especially *S. altissima*. I also made subjective estimates of the relative levels of damage done to goldenrod plants in the two study sites and nearby fields.

Weather data were obtained from the Division of Atmospheric Sciences at Cornell University (Monthly Meteorological Summary, 1976–1977).

RESULTS

Trirhabda adults were much more abundant on *S. altissima* than on *S. juncea* in both years, but were substantially more abundant on both goldenrods in 1977 than in 1976 (Table 1). My subjective estimates of larval abundance agreed with the data on adults.

Solidago altissima plants were shorter and bloomed later in 1977 than in 1976. *Solidago juncea* plants were also shorter in 1977 than in 1976, but in contrast to *S. altissima*, bloomed earlier in 1977 (Table 1). In 1976, taller plants of *S. juncea* tended to bloom earlier than shorter plants; no such relationship existed for *S. altissima*. Product-moment correlations between plant height and date of peak blooming produced coefficients of -0.40 for *S. juncea* ($P < .005$) and 0.15 for *S. altissima* ($P > .3$).

Solidago altissima plants were farther from blooming conspecifics in 1977 than in 1976 (Fig. 1), although the distance between conspecifics, blooming or not, was always 1 dm in both years. *Solidago juncea* showed no major change in distance to blooming conspecifics; in this species, nearest conspecific stems always bloomed (Fig. 1).

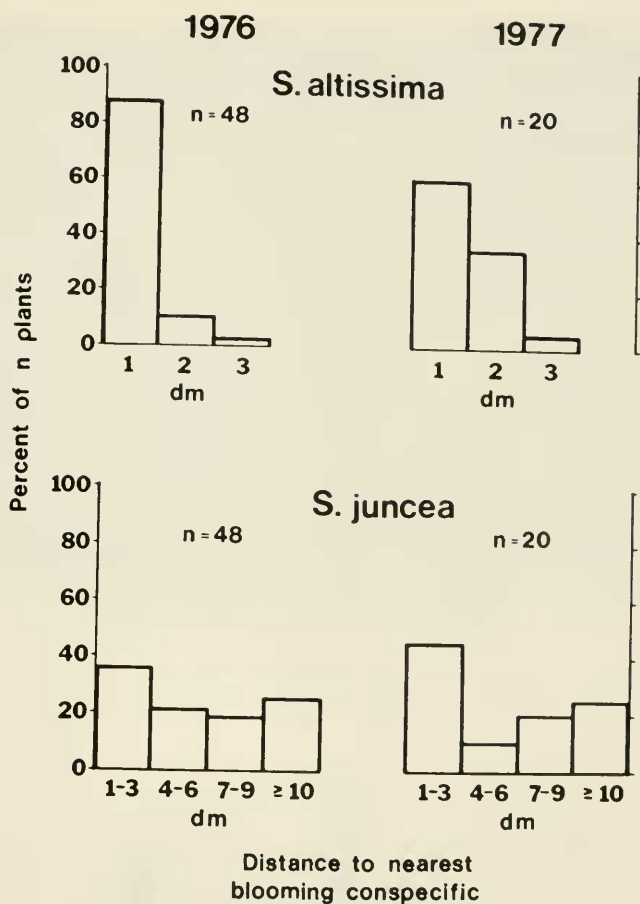


Fig. 1. Distances from marked plants to nearest blooming conspecific plants for *Solidago altissima* and *S. juncea* in 1976 and 1977. For *S. altissima* in both years, the distance to nearest conspecific, blooming or not, was 1 dm for every marked plant (i.e., the density of *S. altissima* stems was the same in both years, but fewer plants bloomed in 1977). In both years, all nearest conspecific stems of *S. juncea* bloomed.

Meteorological information for both years (Fig. 2) shows that, for most months of the growing season, 1977 was warmer than 1976, and that there was about the same amount of total precipitation and total solar radiation in both years. July 1976 and September 1977 had particularly large amounts of rain, and May 1977 had a high total of solar radiation.

A photograph of *S. altissima* stems (Fig. 3) from Field 1 shows the chewing damage done by the larvae (on older, lower leaves) and adults (on younger, upper leaves) of *Trirhabda* beetles in 1977. Damage was not nearly as obvious in 1976.

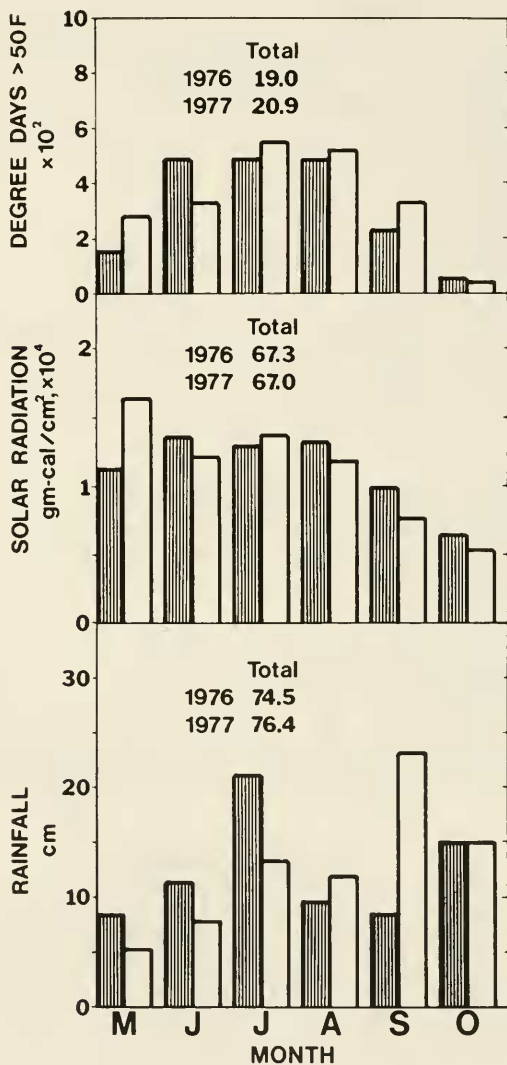


Fig. 2. Monthly meteorological summary data for growing seasons in Ithaca, New York, 1976 (dark bars) and 1977 (open bars).

Both larvae and adults of *Trirhabda* were found feeding along the edges of holes and marginal notches in the leaves, indicating little preference for location in their initiation of feeding. No *Trirhabda* were seen eating stem tissue, and the completely defoliated stems I examined in 1977 showed no damage on the stem itself from chewing insects. Species of *Trirhabda* appear to feed only on leaves.



Fig. 3. Results of herbivory by *Trirhabda* species on two *Solidago altissima* stems in 1977. Larvae fed on the lower leaves, adults on the upper leaves. Note the galls of *Eurosta solidaginis* (Fitch) (Tephritidae) near the top of each stem (see Hartnett and Abrahamson, 1979).

DISCUSSION

Differences between years.—Though the evidence is circumstantial, I see no possible cause for the stunted growth and retarded flowering of *Solidago altissima* in 1977 other than the severe defoliation by *Trirhabda* beetles. The warmer weather of 1977 was, if anything, better for plant growth and development than the weather of 1976, as indicated by the earlier blooming of *S. juncea* in 1977. The inclement weather of September 1977 may have contributed to the lateness of *S. altissima* blooming, but at that late stage of *S. altissima* flower development, high precipitation and low solar radiation probably could not have retarded blooming to the extent observed, especially since September 1977 was warmer than September 1976 (Fig. 2).

By removing large amounts of leaf tissue and photosynthetic area from *S. altissima* plants, the beetles apparently influenced plant growth, flower production, and flower phenology. Shorter stem height and reduced frequency of flower development in 1977 were probably related because stems of *S. canadensis* (and presumably *S. altissima*) will not flower unless they reach a certain minimum size (Bradbury, 1974). Delayed blooming was probably a separate consequence of herbivore damage, because stem height and blooming time were not correlated for *S. altissima* plants in 1976. Late-

blooming plants risk having reduced pollination and fruiting success because of the greater likelihood of cold weather late in September and in early October. Thus, herbivory by *Trirhabda* species seems to have had considerable impact on the sexual reproduction of *S. altissima*.

Asexual reproduction is also important for *Solidago* (Bradbury and Hofstra, 1976; Smith and Palmer, 1976). Multiple-year storage in roots and rhizomes (Bradbury, 1974) certainly buffered the losses to *Trirhabda* to some extent, but could not have entirely eliminated their effect. I did not measure root or rhizome growth in this study, but others have shown a reduction in rhizome production caused by stem gall insects (Hartnett and Abrahamson, 1979). I suspect that species of *Trirhabda* have an even greater effect on underground growth of *Solidago* than do stem gall insects (see Fig. 3).

Other work has suggested that *Trirhabda* numbers vary between years (Balduf, 1929; Capek, 1971; Reid and Harmsen, 1976), but the cause(s) of these population fluctuations remain unclear. Food plant quality may be involved in a feedback control mechanism (see Lomnicki, 1977; Mattson and Addy, 1975; Pimentel, 1961). Abiotic factors could be important, especially those affecting egg survival and larval development rate (Andrewartha and Birch, 1954). The incidence of parasitic attack on species of *Trirhabda* is quite variable (Balduf, 1929; Capek, 1971; Hogue, 1971; Messina, unpublished data; Sholes, 1977), and the predatory pentatomid *Perillus circumcinctus* Stål appears to specialize on *Trirhabda* larvae (Evans, 1980).

Differences between *Solidago* species.—My data and field observations indicate that *Trirhabda* beetles have strong preferences between host species within the genus *Solidago*, as suggested by Reid and Harmsen (1976) and Messina (unpublished data). *Solidago juncea*, *S. nemoralis* Ait. and *S. graminifolia* Salisb. all seem to be eaten much less often by *Trirhabda* in the Ithaca area than is *S. altissima*. The differences in *Trirhabda* numbers on *S. juncea* and *S. altissima* (Table 1) partly reflect the difference between fields; within fields, though, the difference in herbivory on the two species was obvious.

CONCLUSIONS

Trirhabda can retard the stem growth, inflorescence production, and blooming time of *Solidago altissima* (and probably its underground growth as well), but only in years of high population density. When other herbivores are also abundant, such as stem gall insects (Hartnett and Abrahamson, 1979, see Fig. 3), *S. altissima* must experience a considerable reduction in productivity. Despite this reduction, and despite the lesser amount of herbivory on some other sympatric *Solidago* species, *S. altissima* is the most abundant old-field goldenrod in the region surrounding Ithaca, New York

(Sholes, 1980; Wiegand and Eames, 1925). Such success in the face of apparent adversity deserves further, long-term study throughout the range of *Solidago altissima*. Perhaps the years of low *Trirhabda* population density are important to that success.

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